Local processes compound the latitudinal variability in the collapse and recovery of Chilean *Macrocystis integrifolia* populations (Laminariales, Phaeophyceae) following the 1997-1998 El Niño

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Running head: Collapse and recovery of Chilean kelp

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Abstract

An integrated synchronic study was made on the interactive effects of the El Niño Southern Oscillation (ENSO) of 1997-1998 with mesoscale coastal upwelling processes on distribution and abundance patterns of the kelp *Macrocystis integrifolia* at seven locations spread along 1500 km of the Chilean coastline between 18°S to 32° S. The effects of a moderate intensity 1998-2000 La Niña event were included as well. Seasonal monitoring of the adult and juvenile sporophytes was carried out in the field between 1996 and 2000, and correlations were made with the several different climatic indices (MEI, SOI, OET) which have been internationally established for rating the magnitudes and other characteristics of ENSO events. Our own continuous monitoring of sea surface temperatures was used to pinpoint local ENSO events. The ENSO event studied produced high mortalities of *M. integrifolia* at lower latitudes (18°-21°S), associated with decreases in upwelling events. At latitudes near 23°S, the abundance of adult sporophytes decreased during the ENSO without causing local extinctions, correlated with the persistence of upwelling and latitudinal decreases in surface warming. An increase in upwelling in spring 1997 during the ENSO event favored recruitment of juvenile kelp in all the populations observed, although this recruitment did not produce a full recovery in *M. integrifolia* abundance. We concluded from the results that differences are produced by the oceanographic climate in the life strategies of *M. integrifolia* between northern (18°-21°S) and central (30°-37°S) populations in Chile, as well as with congeneric species (*M. pyrifera*) located south of 40°S.

Introduction

Kelp beds persist in a delicate balance among ecological processes driving their development and local extinction. These processes operate over a broad spectrum of temporal and spatial scales (Carlile et al. 1989; Wiens 1989). For *Macrocystis pyrifera,* hierarchically nested scales have been distinguished that are related to the most important factors that explain the spatio-temporal variability of kelp beds (Edwards 2004). The discrimination of scale-dependent variability patterns helps to unify patterns of distribution and abundance with forcing factors operating at given scales (Dayton et al. 1992). Although in population studies the spatial inference is as diverse as the name assigned to the scale occupied, there is consensus about ecological processes, which act on a local scale (10^2-10^3 m), and are subordinated to others acting on a geographic scale (10^6 m), including a significant part of, or the entire latitudinal range of distribution of a species (Levin 1992).

On a local scale, the patterns of distribution and abundance of kelp are the net result of recruitment, growth, and mortality, which are regulated by abiotic and biotic factors (North 1994). Temperature, light and nutrients are the principal abiotic factors controlling population dynamics of kelp (Jackson 1977; Graham 1996; Tegner et al. 1997; Hernández-Carmona et al. 2000); they co-vary exerting synergistic interactions (Kain 1989). Extrinsic biotic factors that affect the kelp dynamics on this scale include competition, herbivory, and epiphytism (Vásquez and Buschmann 1997; Hurd et al. 2000). Intrinsic biotic factors are determined by intraspecific interactions and generate processes of populational self-regulation depending on the carrying capacity of the system (Reed and Foster 1984; Dayton et al. 1984).

On a geographic scale, extension and persistence of kelp beds in the South American Pacific are correlated with the negative thermal anomaly in sea surface temperature (SST) of the coastal branch of the Humboldt Current, which flows towards the Equator (Halpin et al. 2004). This anomalous negative condition is reinforced in spring and summer by the upwelling process of cool subsuperficial water, nutrient-enriched and poor in oxygen (Strub et al. 1998). In coastal areas having prominent geographic features such as points and peninsulas, upwelling may be stable and permanent throughout the year (Martínez et al. 2003). Topographic variability in intensity and frequency of upwelling events is the main source of variation at mesoscale of the SST, and also nutrient concentrations along of this region (Strub et al. 1998). Variability in the SST covaries inversely with the availability of nutrients (Nielsen and Navarrete 2004), generating locality-dependent patterns in distribution and abundance of kelp, other macroalgae, chlorophyll, and consumers (Broitman et al. 2001; Martínez et al. 2003; Vega 2005). Together, these preceding processes generate a cascade-type "bottom up" trophic control, which locally regulates the composition and structure of the biota (Nielsen and Navarrete 2004; Vásquez and Vega 2004), producing a highly diverse mosaic of submarine seascapes. This includes localities where benthic communities are strongly affected by large-scale oceanographic events such as the El Niño Southern Oscillation (ENSO), whereas in other localities the impact of these events is buffered by areas with persistent upwelling (Martínez et al. 2003; Vega et al. 2005).

ENSO is an irregular fluctuation that involves the entire tropical Pacific Ocean and the global atmosphere, generating interannual variability in the oceanographic climate. Variability consists in alternation of periods with positive (El Niño events) and negative (La Niña events) thermal anomalies of the SST in feedback cycles every two to seven years (Fiedler 2002). The changes in oceanographic climate caused by El Niño events have an important role as a process modulator in temperate latitudes of the South American Pacific, producing bathymetric migrations, invasions of exotic species, behavioral alterations, and changes in abundance which can range from reductions in population density to local extinctions (Glynn 1988; Camus 1994), modifying the composition of the biota on local and geographic scales (Camus 2001). Reductions in populations and local extinctions based on conditions generated by El Niño events are important to the "engineer species" (*sensu* Jones et al. 1994) such as kelps, since their presence or absence directly affects the diversity, structure, and functioning of cold temperate coastal ecosystems (Graham 2004; Vásquez J. A. unpubl.).

El Niño events modify the geographic range of distribution of kelp along the latitudinal gradient, generating processes of local extinction correlated with latitude (Camus 1994). Increases in the SST during El Niño decrease the availability of nutrients, producing physiological stress in plants (Zimmerman and Robertson 1985; Gerard 1997). The nutrient deficit increases respiration rates, which in turn increases the rate of tissue erosion above the growth rate, finally producing deterioration and death of sporophytes (Gagne et al. 1982). Also, conditions during El Niño inhibit the growth and reproductive activity of the gametophytes, decreasing or even preventing recruitment (Dean and Deysher 1983; Hernández-Carmona *et al*. 2001). However, local conditions acting on mesoscale may alleviate the effects of El Niño events on some kelp beds, for example, in locations with permanent coastal upwelling (Vega et al. 2005). Persistence of local kelp beds and the post-El Niño transition to a cool, nutrient-enriched condition (La Niña) facilitates and improves recolonization (Edwards 2004), although the recovery process may proceed slowly, often requiring many years (Camus 1994; Martínez et al. 2003).

The 1997-1998 El Niño event on the Northern coast of Chile produced two pulses of positive anomalies in SST, associated with strong poleward flow of warm nutrient-depleted water masses in the first 100 m (Carr et al. 2002). During this event, the thermocline, oxycline and nutricline, normally positioned at 40-60 m depths, were depressed to 150-200 m (Ulloa et al. 2001). Nevertheless, during the 1997-1998 El Niño event, upwelling processes remained active in some coastal localities (Lagos et al. 2002). The 1997-1998 El Niño was immediately followed by a La Niña condition, characterized by a weak to moderate cooling of surface waters from 1998 to 2000 (Takesue et al. 2004). The 1998-2000 La Niña promoted the development of southwesterly winds, which drive coastal upwelling along the South American Pacific coastline (Lagos et al. 2002). Given this scenario of some localities impacted by the 1997-1998 El Niño event, and others relatively unaffected by changing oceanographic conditions, we predicted that kelp beds near at areas with permanent upwelling would persist during and before El Niño conditions, whereas kelp beds away from upwelling areas would experience local extinction and latitude-dependent recolonization processes. In this context, we carried out a monitoring program on seven subtidal populations of *Macrocystis integrifolia* Bory between 1996 and 2000.

Macrocystis integrifolia presents a bipolar distribution on the American Pacific coast, forming beds from the intertidal zone to 15-20 m depth, both in protected and semi-exposed habitats (Vega 2005). In the Southern Hemisphere, the center of distribution of *M. integrifolia* beds is in northern Chile (18°-32° S), although the recorded distributional range for the species ranges from northern Peru (ca. 4º S) to central Chile (ca. 37º S) (Ramirez and Santelices 1991). Our study sites were spread along 1500 km of the north-Chilean coastline, which permitted evaluation of interactive effects between coastal upwelling and an ENSO cycle (1997-1998 El Niño event and 1998-2000 La Niña event) on the dynamics of subtidal kelp beds over a latitudinal gradient between 18° and 32° S.

This study examines in an integrated and synchronous manner, the interactive effects of scale-dependent oceanic processes (ENSO cycle and coastal upwelling) on patterns of distribution and abundance of *M. integrifolia* sporophytes in northern Chile (18-32ºS). Both coastal oceanographic processes are important in the dynamics and organization of populations and communities on rocky shores in northern Chile (Camus 1990, 2001). In general, we postulate that the ENSO cycle and coastal upwelling are forcing agents in the development and persistence of subtidal kelp beds of *M. integrifolia* in the South East Pacific temperate coast.

Methods

Study Area - The study area is located between 18°S and 32°S on the Chilean coast of the South Eastern Pacific Ocean, and has an extension of ca. 1500 Km (Fig.1). On a geographic scale this zone of the Chilean coastline is nearly straight, and is interrupted by a few small peninsulas and semi-protected bays. It is mostly wave-exposed rocky coastline, where SW winds predominate (Strub et al. 1998). On a mesoscale, topographical complexity of the coast is increased by the presence of inshore islands and coastal indentations open to the north, including small points, isthmuses, and peninsulas producing wave-protected sites. Seasonal studies on patterns of distribution and abundance of subtidal *Macrocystis* beds between June 1996 and December 2000 were carried out at seven sites along this coast (Fig. 1A). The geographic location, wave-exposure, and bathymetric distribution of each kelp bed are listed in Table 1. With the exception of the Camarones site (see Results), all kelp beds consisted of a dominant stratum formed by *M. integrifolia* canopies extending to, and spreading at the sea surface. When present, shrub-like plants of the bottom kelp *Lessonia trabeculata* formed a second subsurface stratum (Vega 2005). A third or basal stratum was variable in composition and structure. In some kelp beds, only crustose coralline algae were dominant, or were mixed with a turf of Gelidiales, Ceramiales and/or articulated corallines; others supported monospecific stands or assemblages of foliose macroalgae (Vásquez et al. 2001). There was a high diversity of invertebrates and fishes associated with the kelp beds (Godoy 2000). The most representative herbivores of kelp beds in northern Chile are the snails *Tegula* spp and *Prisogaster niger*, the Decapod Crustaceans

Taliepus spp. and the sea urchins *Tetrapygus niger* and *Loxechinus albus* (Vásquez & Buschmann 1997).

Oceanographic conditions - Consultation with global climatic indices permitted characterization of general oceanographic conditions in the study area between 1996 and 2000, and are useful for making comparisons among oceanographic events and ecological processes which act on different spatio-temporal scales (Stenseth et al. 2003). The warm and cold phases of ENSO were estimated using the Southern Oscillation Index (SOI) and the Multivariate El Niño Index (MEI) obtained from the Australian Metereological Bureau (www.bom.gov.au/climate/current/) and the NOAA climatic diagnostic center (www.cdc.noaa.gov/~kew/MEI/mei.html), respectively. In order to evaluate the interannual and latitudinal variability in thermal anomalies in the study area we used the 1996-2000 SST time series recorded at five Chilean ports including Arica (18ºS), Iquique (20ºS), Antofagasta (23ºS), Caldera (27ºS) and Coquimbo (30ºS) available from the Chilean Navy Hydrographic Service (www.shoa.cl/cendoc-jsp/index.jsp). *In situ* mean water temperatures were obtained at each sampling location using continuous-recording thermographs (Onset Computer Corp., Bourne, Maine, USA), placed at 3 m depth within each kelp bed. Thermal anomalies were calculated from monthly averages of SST for the study area, and from the *in situ* temperature records for each sampling site. For both cases, the mean average monthly anomaly, from January 1996 to December 2000, was calculated as a function of the monthly average of the historical time series over 53 years, obtained from the Chilean Navy Hydrographic Service (www.shoa.cl/cendoc-jsp/index.jsp). To determine the spatial and temporal variability of upwelling events in the study area, we used the monthly average of upwelling index (Offshore Eckman Transport, OET) between 1996 and 2000 for the stations located at 18º, 21º, 24º, 27º and 30º S. The monthly averages were obtained from the Pacific Environmental Laboratory of NOAA (www.pfeg.noaa.gov/products/PFEL/modeled/indices/PFELindices.html; PFEL). A detailed description of the calculation, characteristics, and area of influence of the SOI, MEI and OET indexes for the South American Pacific has been given by Navarrete et al. (2002).

Temporal patterns of abundance - The temporal patterns of abundance in *M. integrifolia* subtidal kelp beds, at each sampling location, were evaluated on a seasonal basis, employing transects perpendicular to the coastline. Sampling was done throughout the entire extension of each kelp bed sampled. Four replicate transects (n=4) were done within each kelp bed, measuring between 50 and 160 m length, depending on the size of the bed, by one meter in width. Juvenile and adult sporophytes of *M. integrifolia* were counted within each transect; abundances of adult and juvenile sporophytes were expressed as density (individuals per m^2). Sporophytes with one or two laminar, lanceolate fronds without sporophylls, and having a holdfast $\leq$ 4 cm were considered to be juveniles (Vega et al. 2005). Seasonal monitoring in rocky habitats at Camarones (18ºS) during the study period was performed to evaluate the potential long-term recolonization of *M. integrifolia*. At the San Marcos site, sampling of an intertidal population of *M. integrifolia* which appeared after the 1997-1998 El Niño, was carried out using the same methodology as described for the subtidal kelp beds.

Data analysis – The robustness of our study is based mainly on the weight of the evidence than on any statistical hypothesis test. This line of thought has been previously applied to kelp population studies where the spatio-temporal variability was dependent on the accessibility, logistics, sea state, diving conditions, and evaluation methods (*e.g.* Tegner et al. 1997; Dayton et al. 1999). These produced discontinuities in the seasonal data collection of kelp abundance at local scale. As a consequence of this, obtained data resulted useless for analysis of variance (ANOVA) or time series analysis. The annual variation of the upwelling index, by latitude, was compared with ANOVA, using SYSTAT 8.0® software for Windows, after subjecting the data to a log + 1 transformation (Sokal and Rohlf 1981). Relations between different climatic indices (SOI, MEI and OET) and local thermal anomalies were determined using Pearson correlation analysis (Sokal and Rohlf 1981).

Results

Oceanographic conditions - The oceanographic climate, based on the SOI and MEI indices, showed normal to slightly cool conditions during 1996, which persisted until summer 1997. From April 1997 to April 1998, the SOI showed negative values due to a high magnitude El Niño event. According to the MEI, the maximum intensities of the El Niño occurred during August/September 1997 (> 2.8 MEI) and February/March 1998 (> 2.7 MEI) (Fig. 1B). Immediately after the anomalously warm condition, the La Niña condition which began in August 1998, was moderately cool (SOI range: 22.4 to –5.5; MEI range: 0.0 to –1.2), and persisted until the end the study period (December 2000). During the winter of 2000, conditions tended towards normality (Fig. 1B). The thermal anomalies calculated as a function of the *in situ* seawater temperature records in all kelp beds studied were negatively correlated with the SOI and positively correlated with MEI (Table 2). During the 1997-1998 El Niño, the positive thermal anomalies in seawater temperature decreased with increasing latitude (Fig. 2). Between 18º S and 21º S the mean value of the thermal anomalies during the El Niño was +2.5ºC, with a winter maximum of 1997 (+2.6ºC) and summer maximum in 1998 (+3.8ºC to +4.4ºC) (Fig. 2). At 23º S, the mean thermal anomaly was +1.9ºC, with a maximum of +2.9ºC in winter 1997 and +2.9ºC in summer 1998 (Fig. 2). In contrast, at 27º S and 30º S the mean value for the thermal anomalies during El Niño was +1.0ºC, with a maximum of +2.1ºC in winter 1997 for both latitudes. A second maximum of +2.2ºC was registered in summer 1998 at 27º S, and +2.0ºC in winter 1998 at 30º S (Fig. 2). No latitudinal pattern was detected in negative thermal anomalies in seawater temperature during the 1998-2000 La Niña condition (Fig. 2). The mean values for thermal anomalies observed during the La Niña condition were -0.2 ± 0.6 at 18º S, -0.6 ± 0.5 at 21º S, -0.4 ± 0.8 at 23º S, -0.7 ± 0.7 at 27º S, and -0.3 ± 0.7 at 30º S. Results suggest moderate cooling at the sea surface during 1998-2000. The lowest negative values for seawater temperature anomalies fluctuated between –1.6ºC and –2.5ºC, and were apparent during different seasons depending on latitude (Fig. 2). The upwelling indices for northern Chile, estimated from the OET for different latitudes within the study area, showed maximum values in spring and summer, reaching conditions near neutrality or with downwelling of surface water in fall and winter (Fig. 2). Annual temporal tendencies in the upwelling index differed significantly with latitude (Table 2). At 21°S the annual temporal tendency of the upwelling index was always significantly lower when compared with all the other latitudes evaluated (Tukey test, $p<0.05$), with the OET reaching negative values during 1998 mainly in fall and winter (Table 3, Fig. 2). This suggests stratification of the water column, and deepening of the thermocline or downwelling. At 18º S, the mean annual upwelling index was significantly lower during 1997, but slightly higher during 1996, 1999, and 2000, than at latitudes greater than 23º S (Table 3, Fig. 2). In contrast, a temporal tendency similar to the OET index was observed at 23º S, 27º S and 30º S (Fig. 2), with a weak but significant latitudinal tendency with increases in the mean upwelling indexes with latitude. This tendency was consistent among years (Table 3). In general, upwelling events during the El Niño condition throughout the study area, mainly in spring 1997 and summer 1998, in part buffered the warming of the sea surface (Fig. 2). This modulation of the effects of 1997-1998 El Niño, increased with latitude due to increasing of frequency and magnitude of upwelling and “dilution” of the El Niño event towards higher latitudes (Fig. 2).

Population dynamics - The 1997-1998 El Niño had varied impact on kelp beds evaluated on the latitudinal gradient included in the present study (18°-32°S). Major impacts of the El Niño conditions were observed in kelp beds located at higher latitudes (18º-21º S), whereas positive thermal anomalies had limited effects in kelp beds at lower latitudes (23º-32º S). As a result, varied spatio-temporal patterns of abundance of *M. integrifolia* were observed in the study area (Fig. 3). During the 1997-1998 El Niño, the density of adult sporophytes in subtidal bottoms at San Marcos (21º S) decreased rapidly and linearly with increasing positive thermal anomalies (Fig. 3). Six months later the site remained completely devoid of adult sporophytes, and no recolonization occurred at the subtidal rocky bottoms within the study period (Fig. 3). In Camarones (18º S) during the 1970's, the kelp bed occupied an area of ca. 40 ha (IFOP 1977), but the 1982-1983 El Niño event caused its disappearance (Soto 1985). Fifteen years later, although the1997-1998 El Niño generated substrate suitable for recolonization (*e.g.* by spores carried by floating kelp) and in spite of favorable development and growth conditions of sporophytes produced by the 1998-2000 La Niña at this latitude, the kelp beds did not become re-established at that time (1998-2000) (Fig. 3). In contrast, the adult portions of the kelp populations from 23º to 32º S persisted in subtidal habitats during the period of positive thermal anomalies of the 1997-1998 El Niño. Within this latitudinal range, the positive thermal anomalies did not significantly affect the abundance patterns of kelp beds situated in areas with permanent upwelling (Constitución, Los Choros and San Lorenzo; Fig. 3). On the other hand, a minor decrease in abundance of adult sporophytes was observed in the kelp beds of Playa Blanca and Los Vilos (Fig. 3), both located in areas without permanent upwelling. During the beginning of the 1998-2000 La Niña, low abundances (≤ 0.01 ind./m^2) of adult sporophytes of *M. integrifolia* were observed at an intertidal site near the subtidal sampling site at San Marcos, where a novel kelp bed was established in the following year and persisted until the end of the study (Fig. 3). In

Constitución, however, the abundance of sporophytes gradually diminished until the kelp bed disappeared in 1999 (Fig. 3), although a few adult sporophytes persisted in the deepest portion of the study site (0.1-0.6 plants/m^2). At higher latitudes (28º-32º S), local abundance of *M. integrifolia* adult sporophytes were temporally stable during negative thermal anomalies (Fig. 3).

With the exception of San Marcos, all subtidal kelp beds evaluated underwent a major recruitment of juveniles during the 1997-1998 El Niño up to the beginning of the 1998 La Niña condition. During subsequent years, a decrease in the abundance of juvenile sporophytes occurred at all the sites evaluated, until 2000 (Fig. 4). The strong increase in abundance of juvenile *M. integrifolia* at all the study sites suggests that the attenuation of positive thermal anomalies induced by increase of upwelling process during spring 1998 favored a synchronous and massive recruitment (Fig. 4). The lower density of juveniles at San Marcos might explain the extinction of the subtidal kelp bed at this site. More still, these cohorts (spring 1997 in all sites) were unable to contribute to the recovery of subtidal kelp beds located in higher latitudes during the following year (Fig. 4). The beginning of the La Niña conditions, indicated by negative thermal anomalies due to increase in seasonal upwelling processes, favored the synchronic development of a second cohort of recruits (fall-winter 1998) at all the study sites, including an emergent intertidal kelp bed at San Marcos (Fig. 4). This cohort could be clearly noted during spring 1998 when the abundance of juvenile sporophytes of *M. integrifolia* showed a second increase in all kelp beds (Fig. 4). Thus, with the exception of Constitucion, the establishment and/or persistence of *M. integrifolia* at the sampling sites, during 1998-2000, appeared to be due to successful recruitments during initiation of La Niña conditions. Conversely, the low but constant abundance of juveniles during 1999-2000 (Fig. 4), suggested that continuous recruitment throughout the year explained stable temporal patterns of abundance of adult fraction in the rest of the kelp populations monitored (Fig. 4).

Discussion

In the design of ecological studies it is of increasing importance to identify the different temporal-spatial scales at which ecological processes act and how these affect relevant population parameters (Dayton and Tegner 1984; Carlile et al. 1989; Levin 1992; Dayton et al. 1999). Some studies have shown the utility of using space as a discrete variable based on *a priori* hypothesis of logistical contrasts by means of a hierarchical sampling design with analysis of variance components (Wiens 1989). This design has been used in studies of scale-dependent process and patterns of dynamics of kelp species (Camus and Ojeda 1992; Edwards 2004). However, when sampling design is unable to fulfill the statistical requisites needed, qualitative analyses can be used, which treat space as a continuum, and data of kelp abundance are collected at randomly selected intervals for indirect identification of scale-dependent processes.

Effects of the ENSO in abundance patterns - Based on the historical record of positive thermal anomalies, those produced by 1997-1998 El Niño have been the strongest ever recorded (Stenseth et al. 2002). As a direct consequence, this event modified the circulation patterns and sea water properties, increasing sea level and isotherm depths (Carr et al. 2002). Also, during this period, the coastal upwelling processes were diminished or inhibited, particularly at low latitudes of the South American Pacific (Ulloa et al. 2001). Additionally, unusually strong swells occurred during winter and spring of 1997 and summer and fall of 1998 (Halpin et al. 2004). These oceanographic conditions caused mass mortalities of adult sporophytes of *M. integrifolia* correlated with latitude, which in many locations resulted in extinctions of local kelp populations (Godoy 2000; Llellish et al. 2001; this study).

The transition and first peak of El Niño conditions generated available substrate, due to decrease in abundance of adult sporophytes. However, the re-establishment of seasonal upwelling process in spring 1997 moderated the water surface warming and nutrient deficit (Carr et al. 2002; Takesue et al. 2004). This relaxation of the El Niño condition favored a synchronic and massive recruitment of *M. integrifolia*, which was reflected by the proliferation of juvenile sporophytes along the Northern Chilean coast. However, this recruitment pulse did not lead to a recovery of populations during the following year, due to a second peak of El Niño conditions in summer 1998. *In situ* experiments showed that recruitment and growth of kelp juveniles during El Niño condition was mainly limited by the availability of nutrients, produced during the positive thermal anomalies of the 1997-1998 El Niño (Hernández-Carmona et al. 2001). This can be considered as circumstantial evidence of the importance in the continuity of seasonal upwelling for the persistence of *Macrocystis integrifolia* populations at low latitudes during El Niño events. The synergistic effect of positive thermal anomalies, reduced availability of nutrients, and increased wave intensity, all acting on a geographic scale, can be buffered at the mesoscale range by other oceanographic processes such as permanent coastal upwelling (Martínez 1999; Vega et al. 2005), producing different stages of development and persistence of local kelp beds over a latitudinal gradient (Vega 2005). Immediately after 1997-1998 El Niño, the South American Pacific coast experienced a period of oceanic conditions which were anomalously cold and nutrient-enriched, termed "La Nina" (Carr et al. 2002, Takesue et al. 2004). The 1998-2000 La Niña event facilitated the recolonization processes of *Macrocystis* beds. However, the recovery rate of populations depended on local factors and on the availability of reproductive propagules (Ladah et al. 1999). The local extinction and recolonization processes produced a change in spatial distribution of the remaining local populations of *M. integrifolia*, similar to what has been described for other South American kelps (Camus 1994; Martínez 1999).

The 1997-1998 El Niño had varied impacts over the latitudinal gradient included in the present study (18°-32°S). The processes of recolonization and recovery of kelp beds are discussed separately: (a) Recolonization: Immediately after 1997-1998 El Niño, recovery of kelp beds between 18º S and 21º S was generally poor and geographically variable. At San Marcos (20º S) recolonization process of kelp bed occurred post-El Niño (albeit recruitment occurred at an intertidal site), whereas the kelp bed documented in 1977 at Camarones (18º S) never became re-established. Local extinction and recolonization processes of *Macrocystis* in Peru were also documented after the1997-1998 El Niño at Paracas (14º S) and Pucusana, extending our results to 12° S (Llellish et al. 2001, Fernandez et al. 2002). The local differences in recolonization processes of kelp beds have been widely associated with availability of microscopic stages (Ladah et al. 1999; Hernández-Carmona et al. 2000, 2001), and survival of low-density patches of adult sporophytes in deepwater refuges (Ladah and Zertuche-González 2004; Vega et al. 2005) or possibly in intertidal areas (present study). During return to cold conditions, with nutrient-rich water and an adequate availability of propagules, local differences in recolonization of kelp beds appear to be the result of variability in factors such as competition with sessile invertebrates, other macroalgae, and substrate availability for settlement (Ladah et al. 1999; Godoy 2000; Llellish et al. 2001; Edwards 2004; Edwards & Hernández-Carmona 2005; Vega et al. 2005). (b) Recovery: This occurred rapidly in kelp beds at high latitudes (23º-32º S) during winter-spring 1998. Six months after 1997-1998 El Niño, all locations (except for San Marcos) evaluated showed recovery, and increase in the abundance of sporophytes. The rapid recovery was facilitated by cool conditions of 1998-2000 La Niña (Ulloa et al. 2001; Takesue et al. 2004), and by the presence of microscopic life stages (Ladah et al. 1999; Buschmann et al. 2004, Vega 2005).

Effects of local factors and mesoscale process in abundance patterns - Under "normal" oceanographic conditions, the kelp abundance is modulated by abiotic factors, as well as by intrinsic and extrinsic biotic factors acting on a local scale (North 1994; Dayton et al. 1984, 1992; Graham et al. 1997; Graham 2002; Buschmann et al. 2004, Vega 2005). In contrast, patterns of distribution and abundance of kelp during 1997-1998 El Niño condition were modulated mainly by oceanographic factors acting on geographic scale (Tegner et al. 1997; Dayton et al. 1998, 1999; Edwards 2004, Vega 2005). During the presently discussed El Niño event, processes acting on mesoscale such as permanent upwelling close to some peninsulas, aided in the local persistence of some *M. integrifolia* populations (Vega et al. 2005). This was the case representing the kelp beds at Constitución (23ºS), where population dynamics of *M. integrifolia* were not modified during the 1997-1998 El Niño because upwelling activity was not interrupted in this area (Lagos et al. 2002; Takesue et al. 2004; Vega et al. 2005; present study). Based on this result it can be suggested that the persistence of kelp populations in the above mentioned upwelling areas during higher positive thermal anomalies might function post-El Niño as local sources which "export" propagules to other localities ("sinks") without upwelling where extinction of kelp may have occurred (Camus 1994). Propagules export may be favored by reproductive sporophylls in floating kelp rafts (Macaya et al. 2005). The return to the processes that had acquired local importance after 1997-1998 El Niño, and during 1998-2000 La Niña, was characterized by the development of different *Macrocystis* population dynamics detectable as a function of the scale of observation employed (geographic, mesoscale, or local). This reveals a scale-dependent differentiation in the relative importance of factors, which determine recruitment, growth, and survival of *Macrocystis* (Edwards 2004, Vega 2005, present study). In this context, numerous studies suggest that these processes are driven by interactions of multiple biological and physical factors which act on mesoscale (*e.g.* ocean temperature, vicinity to areas of coastal upwelling) and on a local scale (*e.g.* availability of reproductive propagules, grazing, and competition) (Reed and Foster 1984; Deysher and Dean 1986; Graham et al. 1997; Tegner et al. 1997; Ladah et al. 1999; Dayton et al. 1999; Hernández-Carmona et al. 2000, 2001; Nielsen and Navarrete 2004; Buschmann et al. 2004; Vega et al. 2005). At Constitución (23º S), increases of sea urchin abundance produced local extinction of *M. integrifolia* under La Niña conditions (Vásquez and Vega 2004). Local, low frequency and stochastic events of this type generate decreasing in kelp abundance, adding a new level of complexity to this dynamic on a geographic scale (Graham 2002, Edwards 2004, Vega et al. 2005).

Hemispherical comparisons - The present study analyzed qualitatively and indirectly the dependence on scale of population dynamics of *M. integrifolia* over a geographic gradient in Northern Chile. Our results complement the analyses of geographic variance presented by Edwards (2004) on the population dynamics of *M. pyrifera* in California upwelling ecosystem. The impact of 1997-1998 El Niño event was catastrophic for *Macrocystis* beds at low latitudes in both hemispheres, with almost complete loss of kelp beds along the coasts of Central and Baja California (Ladah et al. 1999; Hernández-Carmona et al. 2001; Edwards 2004), Peru and the Northern extreme of Chile (Godoy 2000; Llellish et al. 2001; Fernandez et al. 2002, present study).

On the Pacific coast of South America, the almost complete disappearance of kelp beds between 6° and 21°S produced a temporal suppression of the distributional limit of *M. integrifolia* towards high latitudes, similar to that described for *M. pyrifera* in the North American Pacific (Edwards 2004). This pattern has been described for previous El Niño events in both hemispheres (Dayton and Tegner 1984; Soto 1985, Tomicic 1985; Glynn 1988; Camus 1994; Hernandez-Carmona et al. 2001). On the other hand, our results show an important variability in the impact of El Niño on a local scale, suggesting that processes acting locally are relevant along the latitudinal gradient of kelp distribution. Evidence for this, although not analyzed within the context of the current study, can be found in studies of Camus (1994), Camus et al. (1994), Dayton et al. (1998, 1999), Martinez et al. (2003), and Vasquez and Vega (2005). These authors described decreasing of kelp genetic variability and low recovery process at sites located at lower latitudes and the local importance of presence or absence of ecosystem "engineer" (habitat-forming) species.

In conclusion, during 1997-1998 El Niño, the intensity and frequency of coastal upwelling processes were latitudinally modified, interacting inversely with intensity and magnitude of positive thermal anomalies. Persistence of kelp beds in low latitudes occurs only in coastal areas having permanent upwelling. In other areas, El Niño modifies the population dynamics due to inhibition of seasonal upwelling, producing short-term processes of local extinction, and locality-dependent recolonization processes. The permanent upwelling areas play an important role in reproduction and survival of kelp, especially during El Niño events. These areas favor the recolonization process in near areas where massive kelp mortalities occur. Nevertheless, while local patterns of recolonization depend directly on the re-establishment of seasonal upwelling along the Pacific coast of South America, recolonization processes at other locations are more complex, suggesting that the impact of the disturbance intensifies between the extreme Northern Chilean and Peruvian coast (6º-23º S). Alteration of population geographic structure post-El Niño, is transformed into an increase of regional heterogeneity of the distribution and abundance patterns of *M. integrifolia*. This generates differences in the life strategies of *M. integrifolia* between the North (18º-30ºS) and Central (30º-37ºS) regions of Chile or with con-generic species *Macrocystis pyrifera* located in Southern Chile (> 40º S).

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Table 1. Location, degree of exposure, and geographic coordinates of the study sites, with bathymetric distributions of kelp beds of *Macrocystis integrifolia* monitored in northern Chile.). In Camarones during 1970's, the kelp bed occupied an area of ca. 40 ha, but 1982-1983 El Niño event caused the local extinction.

kelp beds of *M. integrifolia*		Geographic coordinates		Bathymetric distributions		Orientation
Locality	site	Latitude S	Longitude W	shallow	deep	of the coast
Camarones	Protected	19°12' 48"	70º 17' 21"	-	-	NW
San Marcos	Exposed	21º 18' 33"	70º 15' 18"	0.5 m	12 m	SW
Constitución	Semi-exposed	23° 26' 30"	71º 36' 30"	1.0 m	15 m	SW
Playa Blanca	Exposed	28º 11' 22"	71º 09' 48"	0.9 m	4 m	NW
Los Choros	Exposed	29º 14' 08"	71º 31' 12"	0.5 m	8 m	SE
San Lorenzo	Protected	30º 21' 30"	71º 40' 30"	0.7 m	5 m	SW
Los Vilos	Exposed	31º 54' 28"	71º 31' 07"	1.0 m	5 m	NW

Table 2. Pearson correlation coefficient (probability in parenthesis), between climatic indices (SOI and MEI) and thermal anomalies calculated from in situ records of seawater temperature of each locality study per latitude. Significant association at alpha = 0.05.

Climatic index	Thermal anomalies from in situ records of seawater temperature per latitude						
	18º	20º	23º	28º	29º	30º	32º
SOI	-0.398	-0.720	-0.733	-0.629	-0.724	-0.466	-0.670
	(0.0017)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0002)	(0.0001)
MEI	0.447	0.858	0.804	0.818	0.769	0.562	0.749
	(0.0003)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)

Table 3. Yearly mean (SD), and upwelling indices (Offshore Eckman transport, $m^3 s^{-1}$ per 100 m of coastline) for quadrants of 3º * 3º of latitude along northern coast of Chile. Result of two-way ANOVA comparing upwelling indices among latitudes and years. Significant differences at alpha of 0.05. (df, degrees of freedom; MS, mean square; *p*, probability level)

Latitude (ºS)	YEAR				
	1996	1997	1998	1999	2000
18º	174.0 (25.5)	49.2 (22.7)	152.3 (38.5)	212.7 (26.6)	214.9 (25.4)
21º	73.0 (32.1)	39.4 (24.2)	-41.3 (53.5)	27.6 (28.5)	75.3 (31.5)
23º	123.2 (13.8)	93.3 (9.7)	125.4 (12.1)	94.3 (8.8)	93.6 (8.2)
27º	153.6 (23.6)	113.6 (13.9)	159.8 (20.3)	123.8 (15.0)	145.3 (20.7)
30º	160.5 (34.0)	127.3 (22.5)	189.2 (37.2)	134.3 (21.7)	168.5 (36.4)

Source of variation	df	MS	*F*	*p*
Year	4	99.339	3.291	0.0118
Latitude	4	741.583	24.567	0.0001
Year * Latitude	16	56.551	1.873	0.0228
Residual	275	30.186		

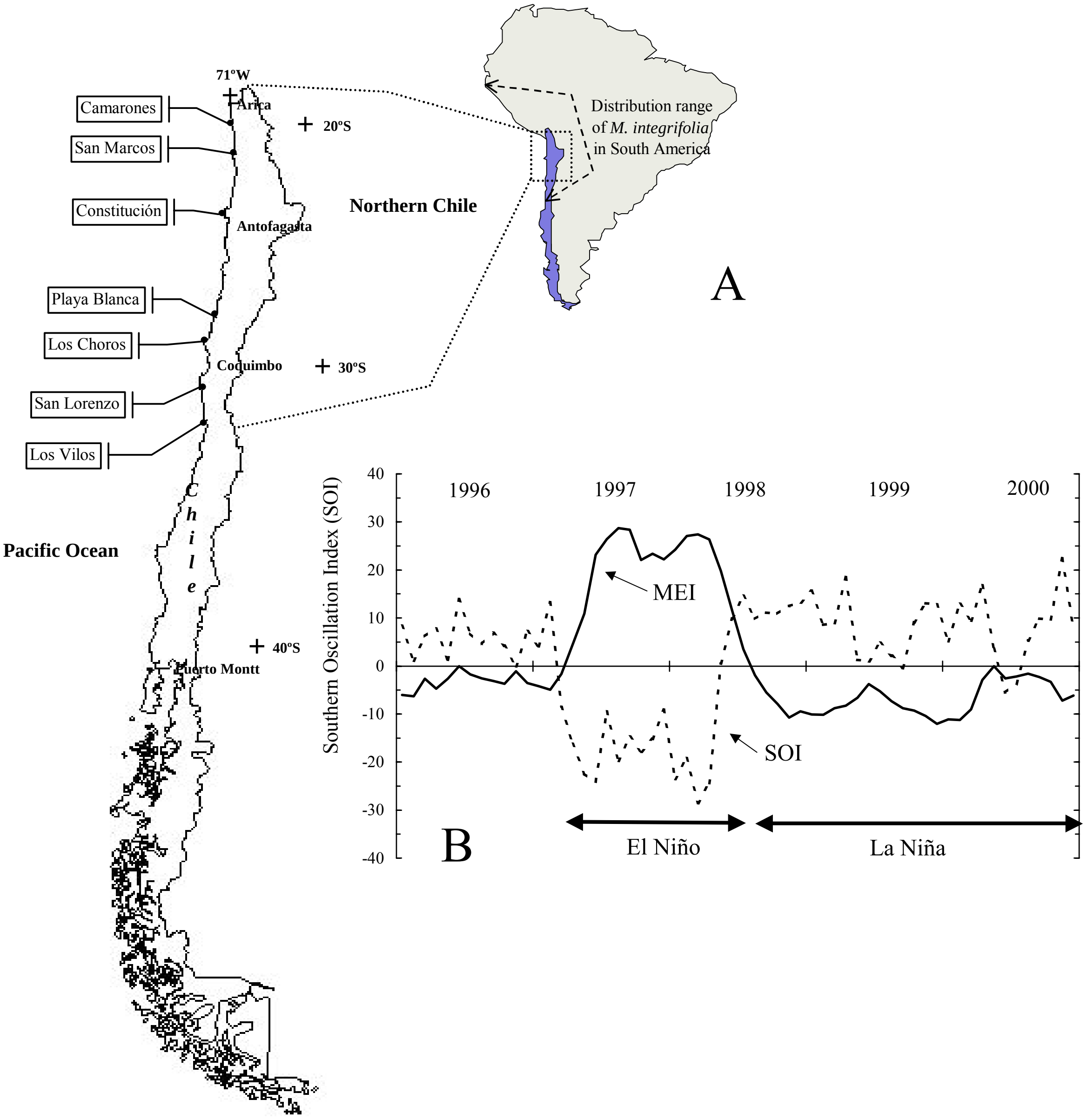
Figure Legends

Figure 1. (A) Study area in northern Chile to show sampling locations and latitudinal distribution of *M. integrifolia* along the South American Pacific coastline. (B) Temporal characterization (1996-2000) of the oceanographic climate in the study area as a function of global climatic indices including the El Niño Multivariate Index (MEI) and the Southern Oscillation Index (SOI).

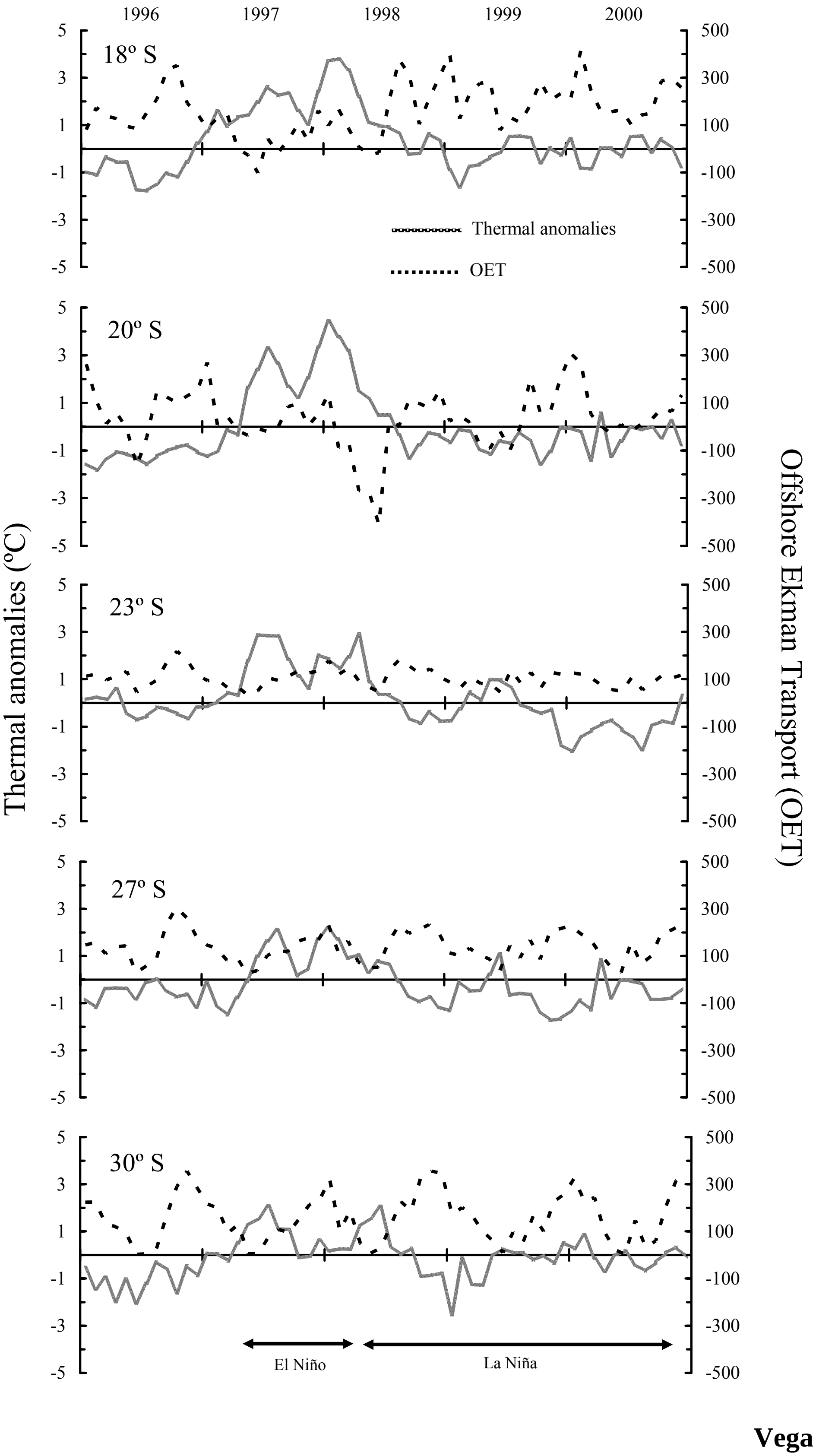
Figure 2. Temporal characterization (1996-2000) of the local oceanographic climate on a latitudinal gradient in northern Chile as a function of thermal anomalies in the sea water temperature (solid line) and the index of coastal upwelling (OET; broken line).

Figure 3. Temporal variation (1996-2000) in the abundances of adult sporophytes of *M. integrifolia* (black circles) and thermal anomalies estimated *in situ* (line) over a latitudinal gradient in northern Chile. *Note*: At San Marcos an intertidal kelp population appeared after an El Niño event (black squares), while the subtidal kelp bed did not recover. At Camarones (top) no sporophytes were observed during the study period.

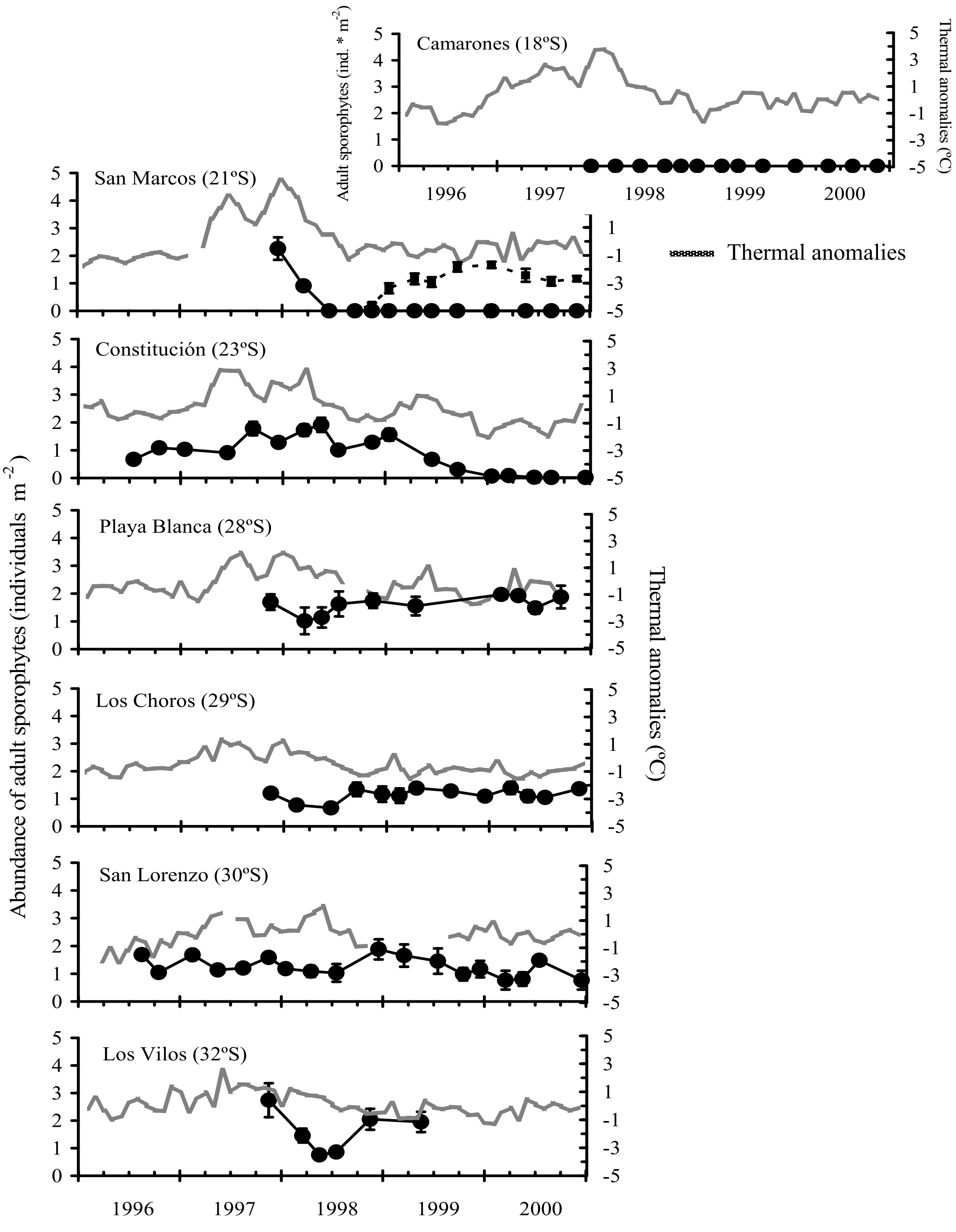
Figure 4. Temporal variation (1996-2000) in the abundances of juvenile sporophytes of *M. integrifolia* (black circles) and thermal anomalies estimated *in situ* (line) over a latitudinal gradient in northern Chile. *Note*: At San Marcos an intertidal kelp population was established post-El Niño event (black squares).



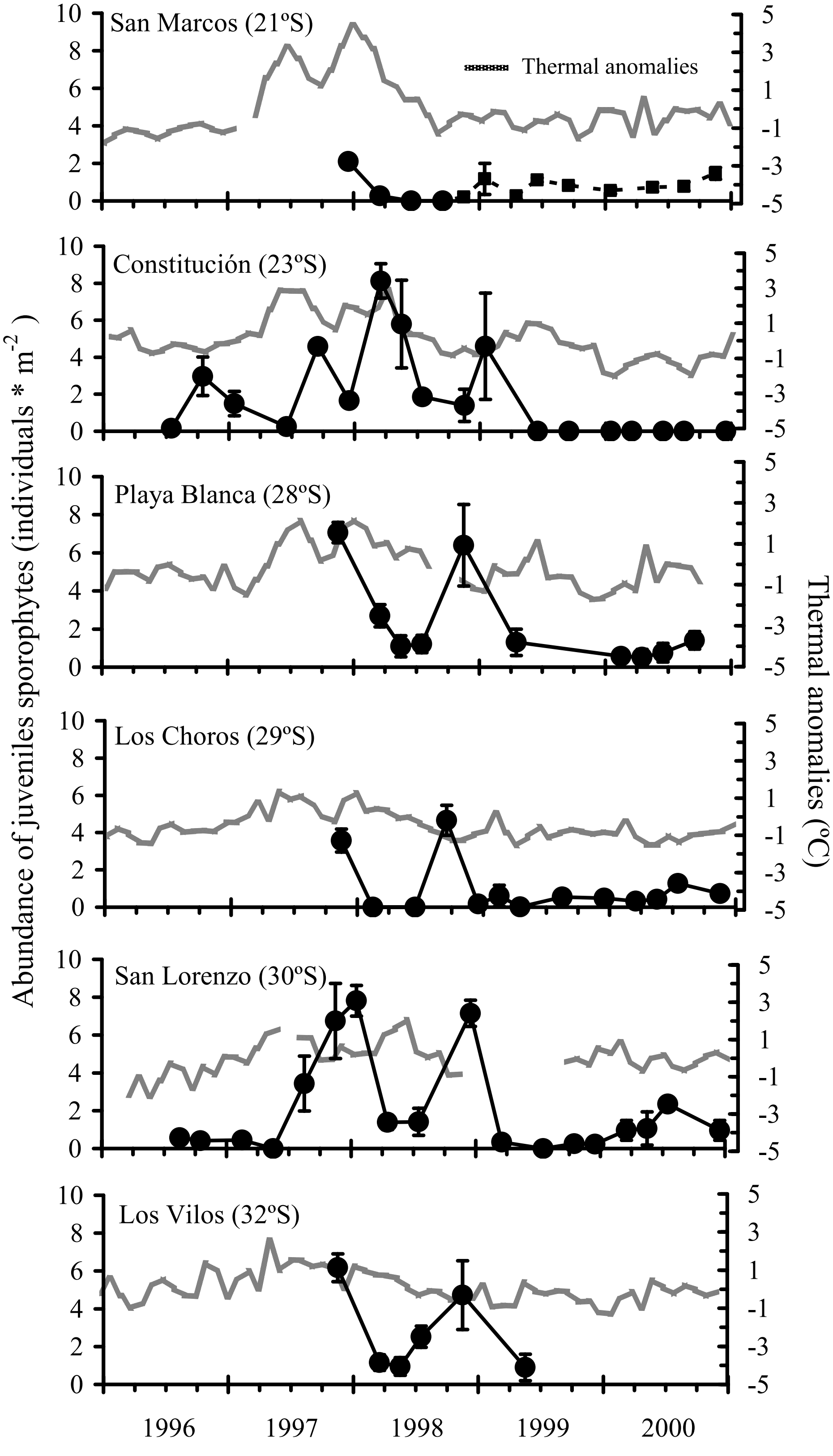
Vega et al. Fig. 1



Vega et al. Fig. 2



Vega et al. Fig. 3



Vega et al. Fig. 4